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Density dependence of avian clutch size in resident and migrant species: is there a constraint on the predictability of competitor density?

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The presence of density dependence of clutch size is tested in 57 long-term population studies of 10 passerine bird species. In about half of the studies of tit species *Parus* spp. density dependence of clutch size was found, while none was found in studies of two flycatcher species *Ficedula* spp. One hypothesis explaining this difference is that migrants are less able to predict the final competitor density, because new pairs are still settling when the first females start laying eggs. Such unpredictability is only a problem for early laying females. If this explanation is true, the commonly observed negative correlation between clutch size and laying date should be stronger in high-density years. I tested this prediction in three populations of Pied Flycatcher *Ficedula hypoleuca*, and compared the results with three populations of Great Tit *Parus major*. In none of the six populations was there a significant correlation between the strength of the seasonal decline in clutch size and population density. Thus the lack of density dependence of clutch size in Pied Flycatchers was not consistent with the idea that this is caused by the unpredictability of final density at the time of egg-laying of the earliest females in the population. Furthermore, density does not have any adverse effect on reproductive output of Pied Flycatchers, and therefore they do not adjust clutch size to density.

Density dependence of clutch size has been observed in long-term studies of a number of bird species, although not in all (for a review, see Sinclair 1989). Several hypotheses have been proposed to explain why population density affects reproduction in some species but not others (Alatalo and Lundberg 1984, Møller 1989, Dhondt et al. 1992, Rodenhouse et al. 1997). Møller (1989) suggested that density dependent reproduction is more often found in migrants because resident species are held at low breeding densities because of high winter mortality. Alternatively, migrant species might not show density-dependent effects on reproduction because they are unable to predict the strength of competition at the time of clutch production (Alatalo and Lundberg 1984). This mechanism might work in migrants that start to breed before all competitors have arrived in the breeding area (Alatalo and Lundberg 1984).

Clutch-size adjustment to local circumstances can only occur if those circumstances are predictable, or limit clutch size directly (Daan and Tinbergen 1997). For early-settling females of a migrant species the competitor density might be unpredictable, because the decision of how many eggs to lay has to be made before all conspecifics have arrived and settled in the breeding area (see e.g. Lundberg et al. 1981). The later the females arrive, the better they will be able to predict the amount of competition for food they will experience when rearing the brood. Thus, if predictability of the final density is important, only late-arriving females will adjust their clutch size to competitor density, and there will be no overall relationship between average clutch size and density.

Comparative analysis of density dependence in clutch size

This section reviews the existence of density dependence of clutch size. Data on the annual mean clutch size and population density were obtained from published long-term population studies of passerine bird species and from unpublished data mainly from the long-term population studies carried out at the Netherlands Institute of Ecology (see van Balen 1973, Drent 1987, van Balen and Potting 1990, Verhulst 1995, and Both 1998a for descriptions of areas and study methods). The studies differed in length from 7 to 41 years. Regression analysis was used to test the effect of population density on the annual mean clutch size for each study separately.

Density dependence of clutch size occurred in 22 out of 57 time series for passerine birds (Table 1). Of the

species examined, all the tit *Parus* spp. populations and the Song Sparrow *Melospiza melodia* are resident, whereas the other populations are migratory. Although there are not enough data to carry out an analysis controlling for phylogeny (Harvey and Pagel 1991), the suggestion is that there is a difference in the likelihood of finding density dependence of clutch size, with one out of five migrant species and five out of five resident species showing density dependence of clutch size in at least one population. Given that all tit species are closely related, as are flycatchers and redstarts, in a comparison of independent groups, one out of three migrants and two out of two residents show density dependence of clutch size. This small sample size is highly biased towards resident and hole nesting species, and therefore it can only serve to generate hypotheses that should be tested with more data.

Tit and flycatcher studies are compared to examine some sample-size effects, because most data are available for these groups. The species have similar breeding ecology, being forest dwelling cavity breeders. In large parts of Europe they occur sympatrically in the same habitat. Twenty of the 42 tit studies reveal density dependence of clutch size, while none of the 11 studies of flycatchers does. One obvious factor affecting the likelihood of finding significant density dependence of clutch size is the length of the time series. For the species from which most data were available, the Great Tit *Parus major*, the probability of finding an effect of density on clutch size (at $\alpha = 0.05$) increased with the length of the time series (logistic regression, $\chi^2_1 = 5.84$, $N = 23$, $p = 0.016$). For the other tit species there was no such effect, which might be due to the lower number of time series available. The flycatcher time series were not significantly shorter than the tit series (means 15.7 and 18.0 respectively, Mann Whitney $U = 192.3$, $N = 51$, $p > 0.50$), which suggests that the absence of density dependence of clutch size is not due to shorter time series. Another potentially confounding factor is the magnitude of variation in density. The coefficient of variation in density was not significantly different between tit and flycatcher studies ($U = 161$, $N = 51$, $p = 0.5$), suggesting that the absence of density dependence of clutch size in the flycatchers is not due to a lack of variation in density. Thus, for the comparison between tits and flycatchers some of the sample-size problems can be ruled out.

Density dependence and timing of breeding

The hypothesis tested is that early breeding flycatchers do not adjust their clutch size to the competitor density because the density at the time of chick rearing is unpredictable. This hypothesis is tested by using three populations of Pied Flycatchers *Ficedula hypoleuca*, studied at the Netherlands Institute of Ecology. An alternative hypothesis making the same prediction is that birds prefer to breed in the best territories, which are occupied first, have an early laying date and a large clutch size. Also under this hypothesis the strength of the laying date effect on clutch size should increase with density. The latter hypothesis will not only apply to migrants, but also to residents. The effect of density on the strength of the laying date effect on clutch size is also examined in three Great Tit populations, breeding in the same areas as the three Pied Flycatcher populations under examination.

In the three areas used in this analysis, density dependence of mean clutch size occurs in all three Great Tit

Table 1. Review of density dependence in annual mean clutch size in long-term studies of passerine birds. The number of studies is based on the number of areas in which population studies have been carried out, single references can include more than one population. Unpublished results are included.

Species			Number of significant studies/total number	Reference
Migratory				
	Barn Swallow	*Hirundo rustica*	1/1	1
	House Wren	*Troglodytes aedon*	0/1	2
	Pied Flycatcher	*Ficedula hypoleuca*	0/9	3–8
	Collared Flycatcher	*F. albicollis*	0/2	9–10
	Redstart	*Phoenicurus phoenicurus*	0/1	6
Resident				
	Great Tit	*Parus major*	12/24	7–9, 11–16
	Blue Tit	*P. caeruleus*	5/13	8, 9, 15, 17
	Coal Tit	*P. ater*	2/4	18–19
	Willow Tit	*P. montanus*	1/1	20
	Song Sparrow	*Melospiza melodia*	1/1	21

1. Møller (1989), 2. Thompson (pers. comm.), 3. Alatalo and Lundberg (1984), 4. Stenning et al. (1988), 5. Virolainen (1984), 6. Järvinen (1987), 7. VWG-Wageningen (unpublished data), 8. Netherlands Institute of Ecology (unpublished data), 9. Sasvari et al. (1987), 10. Török and Toth (1988), 11. Dhondt (1970), 12. von Haartman (1973), 13. Kluyver (1951), 14. Perrins (1965), 15. Perrins (1990), 16. Orell and Ojanen (1983), 17. Dhondt et al. (1992), 18. Lack (1966), 19. Löhrl (1974), 20. Ekman (1983), 21. Arcese and Smith (1988).

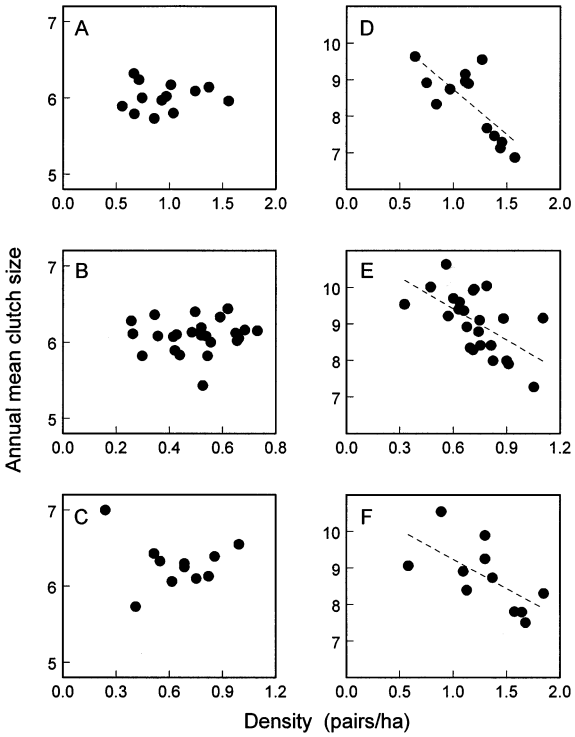

Fig. 1. Effect of population density on the annual mean clutch size of Pied Flycatchers (PF) and Great Tits (GT) in three different areas. Result of regression analysis with clutch size as dependent and density as independent variable: (A) PF Buunderkamp ($F_{1,11} = 0.03$, $p = 0.87$), (B) PF Hoge Veluwe ($F_{1,22} = 0.08$, $p = 0.78$), (C) PF Warnsborn ($F_{1,9} = 0.24$, $p = 0.64$), (D) GT Buunderkamp ($F_{1,11} = 14.2$, $p = 0.003$), (E) GT Hoge Veluwe ($F_{1,22} = 11.6$, $p = 0.003$), (F) GT Warnsborn ($F_{1,9} = 6.45$, $p = 0.03$).

populations, and in none of the Pied Flycatcher populations (Fig. 1). I expressed values in standard deviation units of the means for area and species to compare the density effect between species and areas. This enables comparison without confounding effects of differences in mean and variation in values between species and areas. An ANCOVA examining the effect of species, area and standardized density on standardized annual mean clutch size gave a significant interaction between species and density, showing that the two species indeed differ in the effect of density on clutch size, while within species the populations did not differ in the strength of the effect (species * density interaction: $F_{1,92} = 12.44$, $p = 0.0007$, other interactions were > 0.80). The breeding density of Pied Flycatchers increased strongly during the first 10 years in the Hoge Veluwe population, but excluding these years did not alter the conclusion that clutch size was unrelated to density. Annual mean laying date was not correlated with density in any of the populations, and the species did not differ in this respect (ANCOVA: density: $F_{1,91} = 0.003$, $p = 0.96$, species * density interaction $F_{1,90} = 0.33$, $p = 0.57$). The within year-species-area variance in laying date was not correlated with standardized density, while areas but not species differed (ANCOVA: species: $F_{1,92} = 3.38$, $p = 0.07$, area: $F_{2,93} = 4.18$, $p = 0.02$, density: $F_{1,91} = 0.19$, $p = 0.66$, all interactions $p > 0.20$). This suggests that species did not differ in the extent of competition due to the spread in laying date during the breeding season.

Clutch size has been shown to be related to laying date in both the Great Tit (Kluyver 1951, Perrins 1965, van Balen 1973) and Pied Flycatcher (Lundberg and Alatalo 1992). If predictability of the final density prevents early arriving migrant females from adjusting their clutch size in relation to density, while late females have knowledge of the density, the negative relationship between clutch size and laying date should be more pronounced in years when density is high. Density is in principle predictable for all individuals in resident species at the time of egg-laying, and therefore the date trend is not expected to vary because final density is known to all individuals.

The value of density used in the analyses was the same for all broods in the same year-species-area combination, so that broods could not be treated as independent. The effect of density on clutch size and laying date was therefore analysed in two steps. First the effect of laying date on clutch size was analysed using an ANCOVA in which all nests for both species and three areas were the unit of analysis. Clutch size and laying date were expressed in standard deviation units. In this model the effects of laying date, species, area, and year (included as a factor) on clutch size were analysed. The interaction between year and laying date for each species and area is a test of whether the slope of the laying date effect differs between years. The estimate of the slope between clutch size and laying date for each year-species-area combination was used in the second analysis to test for a correlation between this slope and density. If migrants are constrained by the unpredictability of the final population density, we would expect a negative correlation between the slope and density.

Table 2. Analysis of covariance of laying date effects on clutch size in Great Tits and Pied Flycatchers in three different areas. Clutch size and laying date are expressed in standard deviations units of the species-area mean. Only significant terms are given. Data are for first clutches only. Total number of clutches for Pied Flycatcher and Great Tits is 2594 and 3796 respectively.

Independent variable	Test-statistic	P-value
Year * Species	$F_{23,6242} = 12.9$	0.0000
Area * LD	$F_{2,6242} = 3.49$	0.030
Area * Year	$F_{22,6242} = 2.45$	0.0002
Species * LD^2	$F_{1,6242} = 42.7$	0.0000
Year * Species * Laying date	$F_{22,6242} = 6.62$	0.0000
Year * Species * Area	$F_{24,6242} = 1.53$	0.047

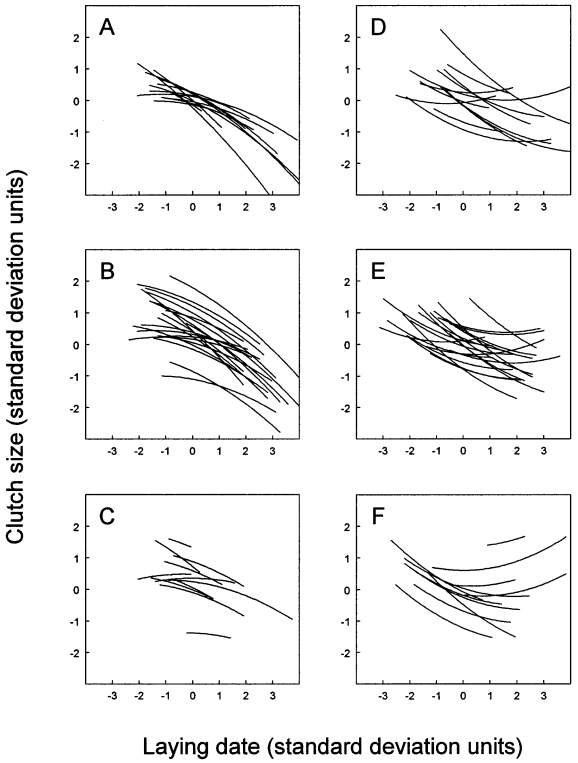

Fig. 2. Fitted curves for the relationship between clutch size and laying date for separate years (see Table 2 for statistics). (A) PF Buunderkamp, (B) PF Hoge Veluwe, (C) PF Warnsborn, (D) GT Buunderkamp, (E) GT Hoge Veluwe, (F) GT Warnsborn. PF = Pied Flycatcher, GT = Great Tit.

ANCOVA was performed using GLIM. To account for possible non-linear effects a quadratic term for laying date was included in the analysis. The analysis was started with laying date, its quadratic term, year, species, area and all interaction terms. Significance was tested by excluding the terms in a hierarchical order, and the change in deviance used to calculate F-ratios. Only the significant terms of this analysis are given.

The relationship between clutch size and laying date differed between years, areas and species (Table 2). Within species, areas resembled each other in the within-year effect of laying date on clutch size (no significant 4-way interaction of year, area, species and laying date), although the absolute laying date effect differed between areas (area * laying date interaction). The significant three-way interaction species * year * laying date shows that the two species differed both within and between years in how laying date affected clutch size (Fig. 2). The quadratic laying date term differed between species, but not between years and areas. Because the quadratic laying date term did not differ between years, we can use the estimates for the linear term to describe between-year differences in the laying date effect on clutch size. In none of the six populations was the estimate of the slope of laying date on clutch size significantly correlated with population density, and species and areas did not differ in this respect (Fig. 3). The prediction that the laying-date effect is stronger in migrants in years of higher density, and that they differ in this respect from residents is thus not met for these two sympatric species. Predictability of final population density thus does not seem to be the constraint preventing the migrant Pied Flycatcher from adjusting clutch size to density.

Additional support for the conclusion that predictability of density is not the constraint in migrant Pied Flycatchers comes from analyses of density effects on reproductive output. If density has adverse effects on Pied Flycatcher reproduction, but flycatchers cannot optimally adjust clutch size to density because density is unpredictable, we would expect a negative correlation between reproductive output and density. In none of the three flycatcher populations did we find a negative correlation between the number of first clutch fledglings and density, nor between the proportion of chicks fledged and density (Fig. 4). In contrast, the Great Tit populations showed a negative correlation between

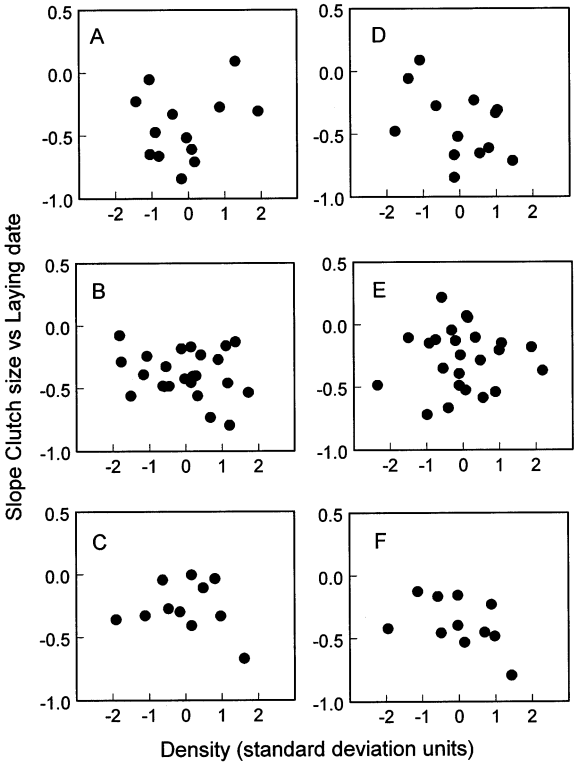

Fig. 3. Relationship between the linear regression coefficient of clutch size on laying date and population density. (A) PF Buunderkamp, (B) PF Hoge Veluwe, (C) PF Warnborn, (D) GT Buunderkamp, (E) GT Hoge Veluwe, (F) GT Warnsborn. ANCOVA: standardized density $F_{1,91} = 1.34$, $p = 0.25$, species: $F_{1,91} = 0.37$, $p = 0.34$, area: $F_{2,91} = 1.94$, $p = 0.15$, density * species: $F_{1,86} = 0.65$, $p = 0.42$, density * species * area: $F_{2,84} = 1.95$, $p = 0.15$. Other interactions: $p > 0.75$. PF = Pied Flycatcher, GT = Great Tit.

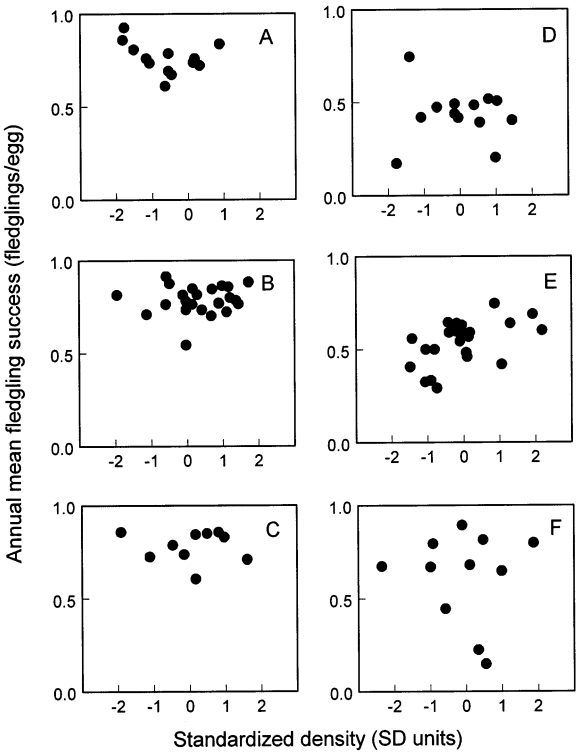

Fig. 4. Effect of population density on the annual mean fledging success (number of fledglings/number of eggs per nest) of Pied Flycatchers (PF) and Great Tits (GT) in three different areas. (A) PF Buunderkamp, (B) PF Hoge Veluwe, (C) PF Warnsborn, (D) GT Buunderkamp, (E) GT Hoge Veluwe, (F) GT Warnsborn. Logistic regression of all species-plot-year combinations on fledgling number/clutch size: species differed ($\chi^2_1 = 6.63$, $p = 0.010$), but areas were not different, and no effect of density was found, neither any interaction with density (all p-values > 0.74). PF = Pied Flycatcher, GT = Great Tit.

fledgling number and density (ANCOVA on standardized values: species * density interaction, $F_{1,90} = 5.29$, $p = 0.024$). Great Tits and Pied Flycatchers did not differ in the (lack of) effect of density on nestling survival (Fig. 4).

Discussion

Density dependence of clutch size was found in about half the long-term studies on resident tits, and in none of the studies on migratory flycatchers. It was also found in one other resident and one other migratory species, while two other migrant species showed no significant effect of density. These data suggest that the pattern is more common in resident than in migrant species. Møller (1989) concluded the opposite from a review based on a smaller number of studies, and suggested that due to strong competition in winter, resident species breed mostly below density levels at which competition occurs. Several studies have shown that winter survival depends strongly on density in resident species (Krebs 1970, Ekman 1984, Tinbergen et al. 1985, Arcese et al. 1992, Both et al. 1999). However, population levels are not reduced enough to prevent competition during breeding, otherwise density dependence of clutch size would not be expected (see Arcese and Smith 1988). In contrast, the review suggests that migrants might not show density-dependent reproduction because their numbers are below levels at which competition occurs.

In three sympatric populations of Pied Flycatchers and Great Tits mean clutch size of flycatchers was not correlated with density, whereas mean clutch size of Great Tits was negatively correlated with density. In none of those six populations was the effect of laying date on clutch size significantly stronger in years with a high density. Furthermore, there was no density effect on reproductive output in flycatchers, suggesting that density has no adverse effect during reproduction in this species, whereas it has in Great Tit populations. This indicates that the lack of density dependence of clutch size in the migratory Pied Flycatcher was not due to unpredictability of the final breeding density, and that density is not an important determinant of reproductive success.

Density dependence of clutch size is analysed in this paper using correlations from long-term studies. However, such analyses do not necessarily indicate a causal relationship, because resource levels and density might be correlated. Experiments in Great Tits in which the density was altered experimentally have corroborated a causal relationship between clutch size and density (Kluyver 1951, Both 1998b) whereas experiments in Pied Flycatchers have not (Tompa 1967, Alatalo and Lundberg 1984, and a similar result for the closely related Collared Flycatcher *Ficedula albicollis*, Török and Tóth 1988). Thus, the pattern reported here based on correlational studies is also found in experimental studies.

Density dependence of clutch size is expected if selection pressures associated with density shift the optimal clutch size downwards as density increases (as shown by Both et al. 2000), and if the density is predictable at the time of egg-laying. The data presented here suggest that lack of predictability does not explain the lack of density dependence in Pied Flycatchers, and we provided evidence for the alternative explanation that reproduction is unaffected by density, suggesting that selection for clutch size is independent of the density of conspecifics. In both Pied and Collared Flycatchers nestling survival rate and nestling growth decrease slightly as breeding density is manipulated to be very high, especially in years with adverse weather conditions (Alatalo and Lundberg 1984, Török and Tóth 1988). This suggests that com-

petition for food in flycatchers is sometimes affected by density, but because this is mediated by unpredictable weather conditions the birds might not be able to adjust their clutch size. In contrast, selection pressures on clutch size are strongly density dependent in the resident Great Tit (Kluyver 1951, Krebs 1970, Tinbergen et al. 1985, Both 1998a) causing the optimal clutch size to decline with density (Both 1998c, Both et al. 2000). Clutch or brood size manipulations in years or areas with different densities should reveal the fitness consequences of alternative clutch sizes under different densities, and test the hypothesis that the 2optimal clutch size of flycatchers does not change with density.

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